

Expansion of Direction Space around the Cardinal Axes Revealed by Smooth Pursuit Eye Movements

Anton E. Krukowski^{1,2} and Leland S. Stone^{1,*}

¹Human Factors Research and Technology Division
NASA Ames Research Center
Moffett Field, California 94035

²Department of Psychology
San Jose State University
San Jose, California 95192

Summary

It is well established that perceptual direction discrimination shows an oblique effect; thresholds are higher for motion along diagonal directions than for motion along cardinal directions. Here, we compare simultaneous direction judgments and pursuit responses for the same motion stimuli and find that both pursuit and perceptual thresholds show similar anisotropies. The pursuit oblique effect is robust under a wide range of experimental manipulations, being largely resistant to changes in trajectory (radial versus tangential motion), speed (10 versus 25 deg/s), directional uncertainty (blocked versus randomly interleaved), and cognitive state (tracking alone versus concurrent tracking and perceptual tasks). Our data show that the pursuit oblique effect is caused by an effective expansion of direction space surrounding the cardinal directions and the requisite compression of space for other directions. This expansion suggests that the directions around the cardinal directions are in some way overrepresented in the visual cortical pathways that drive both smooth pursuit and perception.

Introduction

The cortical visual pathway in the primate brain has been described as having two major branches—the dorsal and the ventral “streams” (Ungerleider and Mishkin, 1982). It has been proposed that these streams subserve separate functions, vision for action and vision for perception, respectively (Goodale and Milner, 1992; Ganel and Goodale, 2003), although others have argued against this view (e.g., Stone et al., 2000; Smeets et al., 2002; Dassonville et al., 2004), in particular for oculomotor action (for a review, see Krauzlis and Stone, 1999). Both the putative locus of the divergence and the degree of independence between these two functional streams are topics of continuing debate. There is general agreement that the middle temporal area (MT) and the medial superior temporal area (MST), two cortical areas in the dorsal stream, are involved in both motion perception and pursuit (e.g., Newsome et al., 1985, 1988; Newsome and Pare, 1988; Dursteler and Wurtz, 1988; Komatsu and Wurtz, 1988, 1989; Salzman et al., 1992; Pasternak and Merigan, 1994; Rudolph and Pasternak, 1999; Ilg and Theier, 2003), but previous physiological studies have not

established whether the same or independent signals within these areas drive perception and pursuit.

Studies that measure psychophysical and motor performance offer an opportunity to measure the degree to which perception and action respond to the same neural signals, as opposed to independent neural channels colocalized within the same cortical region. Our approach is to make use of the well-established perceptual phenomenon that direction discrimination exhibits a robust directional anisotropy known as the oblique effect (e.g., Ball and Sekuler, 1987; Heeley and Buchanan-Smith, 1992; Gros et al., 1998). We recently found similar perceptual oblique effects both when human observers pursue a moving target and when they maintain stationary ocular fixation (Krukowski et al., 2003). During ongoing pursuit, the neural signal responsible for the perceptual oblique effect must therefore include an anisotropic motor corollary signal, because there is little consistent residual retinal motion. This psychophysical finding suggests that the neural signal driving pursuit itself might also show an oblique effect.

Here, we compare direction judgments and pursuit responses made simultaneously to the same motion stimuli to see if perception and action exhibit similar anisotropies. The existence of such a shared signature peculiarity in direction processing would provide strong evidence for a shared motion signal driving both perception and pursuit. Furthermore, while forced-choice psychophysical procedures measure the overall oblique effect (an anisotropy in the signal-to-noise ratio of the direction information driving perceptual decisions), eye-movement measurements afford the possibility of dissecting this anisotropy into its signal and noise components and thus shedding light on the underlying mechanism.

We present here the results of a series of experiments demonstrating that, under a wide range of experimental conditions, a similar directional anisotropy is observed in both perception and pursuit. The mechanism underlying the pursuit oblique effect is an expansion of direction space surrounding cardinal directions and the requisite compression of space for other directions. Our findings demonstrate that both perception and pursuit are limited by similar direction anisotropies, most likely due to shared cortical motion processing signals through the superior temporal sulcus.

Results

In experiment 1, we measured the precision of the perceived direction of motion and the direction of the pursuit response in the same trials within a two-interval forced choice (2-IFC) paradigm (Figure 1A). Eight observers were asked to track with their eyes sequentially paired presentations of a small, moving spot and to report the interval that contained the more clockwise direction of motion (e.g., the blue arrows in Figure 1A). From the binary perceptual decisions, we generated psychometric curves. To derive a comparable metric

*Correspondence: lstone@mail.arc.nasa.gov

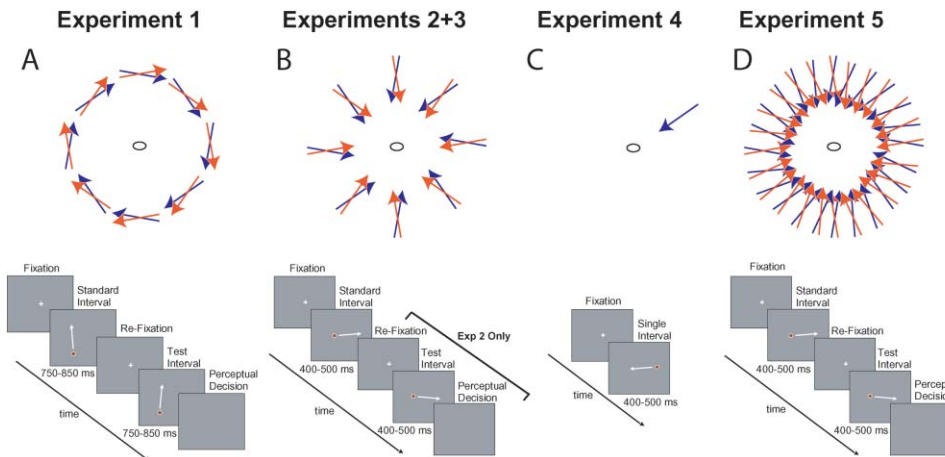


Figure 1. Experimental Design

(A), (B), (C), and (D) illustrate the procedures in experiments 1, 2–3, 4, and 5, respectively. The top illustration in each panel represents the range of stimulus directions presented within a single block. The bottom illustration in each panel represents the temporal sequence for a sample trial from a single block. In experiment 1 (A), target motion was always tangential at 10 deg/s. In experiments 2–5, (B–D), target motion was always radially inward at 25 deg/s. Experiments 1, 2, and 5 (A, B, and D) were 2-IFC experiments with each red-blue pair of overlapping arrows representing the target motions of the two intervals within a single 2-IFC trial. Observers were asked to indicate which interval (first or second) contained the motion that was in a more clockwise direction (i.e., the blue arrow for each pair). In experiments 1 and 2, all four cardinal directions and four primary oblique directions were randomly interleaved in a single block, while in experiment 5, all possible directions were presented. Experiments 3 and 4 (B and C) were single stimulus interval pursuit-only experiments with no psychophysical task. In experiment 3 (B), all four cardinal directions and four primary oblique directions were randomly interleaved in a single block. In experiment 4 (C), one direction of motion was presented repeatedly within each block (i.e., there was no directional uncertainty).

for perception and pursuit, we converted the pursuit response into a single binary “pursuit decision” (see Experimental Procedures; Beutter and Stone, 1998; Stone and Krauzlis, 2003). Figure 2 shows the typical oculomotor responses of a single trial (Figure 2A) with the desaccaded pursuit speed and direction traces (Figure 2B). The initial pursuit directions for the two intervals in the first 150 ms after pursuit onset (downward arrow), the so-called “open-loop” period (Lisberger and Westbrook, 1985), were then converted into a binary answer to the question: Is the pursuit direction during the test interval more clockwise than that during the standard interval? The probability of a clockwise pursuit decision was computed for each possible direction difference between the test and standard intervals and was then used to generate “oculometric curves” (see Experimental Procedures). Sample psychometric and oculometric curves for a single naive observer are shown in Figures 3A and 3B. Both the raw psychophysical and oculometric data show an oblique effect; the curves are steeper for motion along the cardinal axes than for motion along the oblique axes.

The trends shown in Figures 3A and 3B held for all observers. Direction thresholds for cardinal versus oblique motion are shown in Figures 3C and 3D, computed from the psychometric and oculometric curves. All data points lie above the line of slope 1 and intercept 0. Across observers, the difference between cardinal and oblique thresholds was highly significant for both perception [$t(7) = 8.669$, $p < 0.001$; paired, one-tailed] and pursuit [$t(7) = 3.207$, $p < 0.007$; paired, one-tailed]. Furthermore, the strength of this oblique effect was similar for both perception and pursuit. The mean (\pm SD across observers) ratios of oblique to cardinal thresh-

olds were 2.0 ± 0.4 for perception and 2.0 ± 0.8 for pursuit, which are statistically indistinguishable [$t(7) = 0.088$, $p > 0.932$; paired, two-tailed].

The above analyses are specific to the initiation of pursuit, or the “open-loop” response, which is of particular interest because it is the response to the initial visual motion signal that drives pursuit before feedback from the eye movement itself has a chance to affect the retinal stimulus (Lisberger and Westbrook, 1985). However, we also found a clear oblique effect during steady-state pursuit when efference-copy feedback signals dominate the pursuit response (Lisberger et al., 1987; Newsome et al., 1988; Stone and Lisberger, 1990). We analyzed the pursuit response in the window 350–500 ms after pursuit onset (see Figure 2C, upward arrow) and, across observers, the difference between cardinal and oblique thresholds remained significant [$t(7) = 4.693$, $p < 0.001$; paired, one-tailed].

In experiment 2, we varied the experimental design to determine the robustness of the pursuit oblique effect and to allow direct comparison of the results with those of an earlier study (Churchland et al., 2003). The target speed was increased from 10 deg/s to 25 deg/s, and the trajectory was directed toward the point of fixation rather than tangential to the point of fixation (Figure 1B). The latter change enabled us to limit the analysis to presaccadic pursuit; the radial trajectory was designed to delay and sometimes to eliminate catch-up saccades. The task design followed that of experiment 1, such that a 2-IFC perceptual task was performed at the same time and a large number of target trajectories were interleaved to minimize a priori knowledge about target direction.

All five observers showed a clear oblique effect for

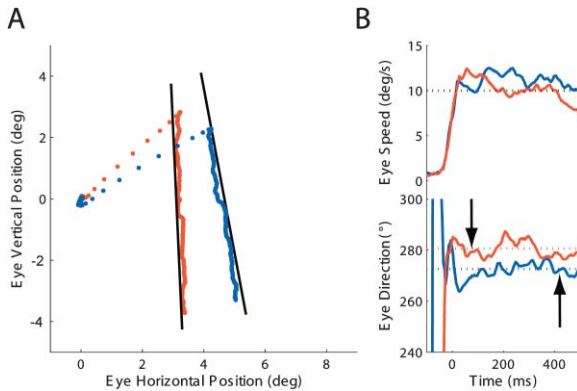


Figure 2. Example Trial with Raw Eye Movement Response

(A) Eye position trajectories for the two intervals of target motion for a single trial from experiment 1 with naive observer cd. The target trajectories are shown in black, and the eye trajectories for the first and second intervals are shown in blue and red, respectively. (B) Eye velocity (desaccaded and 150 ms boxcar filtered) time courses for the same trajectories as in (A), plotted in polar coordinates (speed [top] and direction [bottom]). Eye speed and direction are shown for the first (blue) and second (red) intervals. Target directions for the first and second intervals are shown in the bottom panel as horizontal dashed lines in blue and red, respectively. The time axis is aligned to this observer's mean pursuit latency (180 ms after target motion onset). Eye speed accelerates rapidly up to a robust steady-state response, sometimes even greater than the target speed of 10 deg/s shown with the horizontal black dashed line. The time point for the open-loop analysis is marked by the downward arrow 75 ms postpursuit onset, which, due to the boxcar filtering, is the average velocity in the first 150 ms after pursuit onset. The time point for the steady-state analysis (425 ms) is marked by the upward arrow and corresponds to the interval 350 to 500 ms postpursuit onset. Both decisions are counterclockwise, i.e., the test interval (blue) is more counterclockwise. Note that the oculometric decision would have been identical at any time point after pursuit onset.

perception and pursuit (Figure 4). When oblique thresholds were plotted against cardinal thresholds, once again all data points lay above the line of slope 1 and intercept 0. Across observers, the differences between cardinal and oblique thresholds were significantly different for both perception [$t(4) = 2.908$, $p < 0.022$; paired, one-tailed] and pursuit [$t(4) = 2.825$, $p < 0.024$; paired, one-tailed]. The mean (\pm SD across observers) ratios of oblique to cardinal thresholds were 1.8 ± 0.5 for perception and 1.7 ± 0.5 for pursuit, and the two are statistically indistinguishable [$t(4) = 0.056$, $p > 0.958$; paired, two-tailed]. These results show once again that both pursuit and perception reveal a clear oblique effect, despite the change in target speed and trajectory.

Two other factors in experiments 1 and 2 are of particular interest because of their possible role in eliciting cognitive and attentional influences on pursuit that might account for the presence of the oblique effect: (1) the uncertainty in stimulus direction and (2) the linking of the oculomotor task with a perceptual task. We ran two more experiments to test for the influence of these two factors.

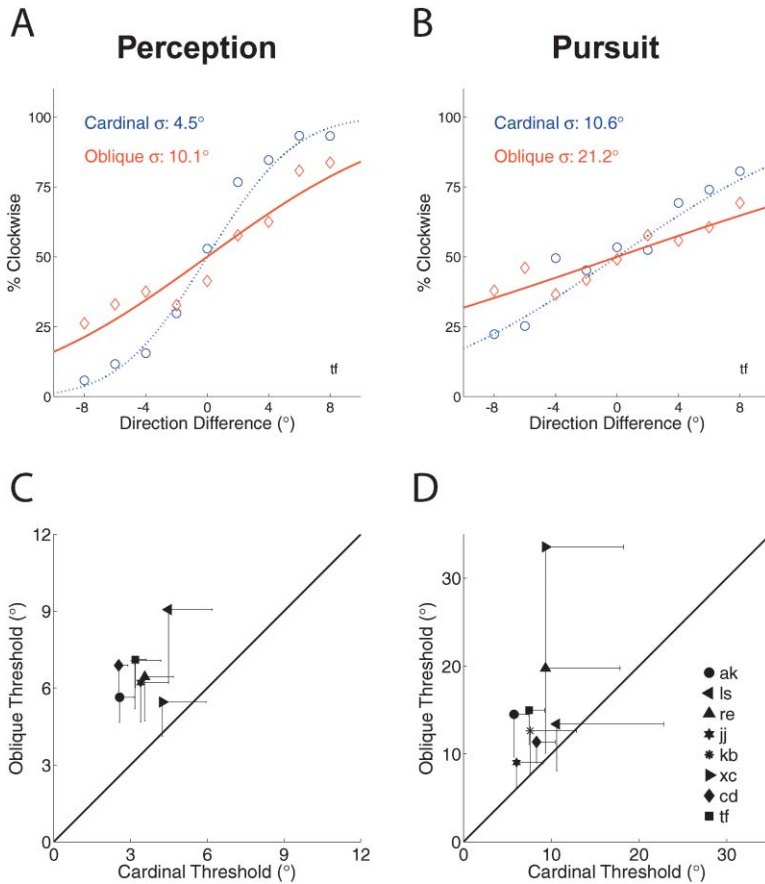
Experiment 3 was conducted with significant uncertainty in stimulus direction, but without a perceptual task. The stimulus trajectories were identical to those in single intervals from experiment 2, and observers

were asked simply to track the stimulus with their eyes. All four observers exhibited a clear oculomotor oblique effect, despite the lack of a perceptual task. When oblique thresholds are plotted against cardinal thresholds, once again all data points lie above the line of slope 1 and intercept 0 (Figure 5A). Across observers, cardinal and oblique thresholds were significantly different [$t(3) = 3.665$, $p < 0.018$; paired, one-tailed]. The mean (\pm SD across observers) ratio of oblique to cardinal thresholds was 1.7 ± 0.2 .

Experiment 4 was run without any directional uncertainty and without any perceptual task; the direction was blocked such that the target direction was completely predictable within each block of trials (Figure 1C). Three observers still showed a similar oblique effect as before (solid symbols in Figure 5B). Across observers, cardinal and oblique thresholds were significantly different [$t(2) = 7.359$, $p < 0.009$; paired, one-tailed]. The mean (\pm SD across observers) ratio of oblique to cardinal thresholds was 1.6 ± 0.2 .

Experiment 4 demonstrated that neither the presence of the perceptual task nor the presence of stimulus uncertainty is necessary to reveal a pursuit oblique effect. This was somewhat surprising given that a recent study (Churchland et al., 2003) found little evidence for an oblique effect for pursuit under similar conditions. We therefore reanalyzed our data from experiment 4, examining only the three canonical directions tested by Churchland and colleagues (straight leftward, straight downward, and downward and leftward). When limiting our analysis to these directions only (open symbols in Figure 5B), we found that the oblique effect was eliminated for one observer, such that the effect across observers was no longer significant [$t(2) = 1.315$, $p > 0.159$; paired, one-tailed].

Our data so far clearly establish that pursuit has a directional anisotropy quantitatively similar to the oblique effect for simultaneously measured perceptual judgments. What can account for this oblique effect? Why are small differences in target motion surrounding cardinal directions more salient than those surrounding oblique directions? The oculometric threshold is essentially a measure of the signal-to-noise ratio (SNR) of the neural information about direction that is available to make the decision. Because the eye movement traces give us full access to both the signal and the noise, we can examine to what extent each contributes to the overall SNR or threshold. Consider a pair of target motions that are close to each other, e.g., at 0° (directly to the right) and at 2° (pointed slightly upward from the pure rightward direction). The noise is the precision of each neurally encoded direction sample (i.e., the error bar on the two encoded directions in the 2-IFC). The signal is the effective separation of the means of the two encoded values (i.e., the average size of the difference between the two encoded directions, which one might assume would be close to the veridical value of 2°). A signal greater than 2° would indicate an expansion of direction space, and a signal smaller than 2° would indicate a compression of direction space. Pursuit directions will be more distinguishable around the cardinal directions (i.e., will show greater SNR) if either the signal is larger and/or the noise is smaller than for oblique directions.



To fully map the encoding of direction space for pursuit, we ran a final experiment using all possible directions rather than just clusters of directions around the eight cardinal and principal oblique directions (Figure 1D). To decompose the pursuit oblique effect into separate signal and noise effects, we plotted pursuit direction as a function of target direction for all trials. Figure 6 shows the raw data for a single naive observer. Note that perfect performance would entail a straight line of slope 1, but that the data show a thick, wiggly line that, on average, has a slope of 1.01. The direction gain, the local slope of the data and a measure of the local signal strength, appears to modulate quas sinusoidally around a mean of 1. The direction semi-interquartile difference,

or Just-Noticeable Difference (JND), a measure of the vertical thickness of the line and of the local direction noise, appears largely constant across directions.

All four observers showed expansion of direction space surrounding cardinal directions and the requisite compression at the primary oblique directions, but little variation in direction noise across direction (Figure 7). The left column of Figure 7 shows the direction gain as a function of target direction for all four observers tested. Note that direction gain for all observers shows 4-fold symmetry locked on the cardinal directions. A circular Fourier analysis confirms this fact by showing that the frequency spectra of the direction gain curves were dominated by the fourth harmonic and were phase

Figure 3. Perceptual and Pursuit Thresholds from Experiment 1

(A and B) Raw psychophysical (A) and oculometric (B) curves for naive observer tf. The blue curves indicate cardinal motion, and the red curves indicate oblique motion. In both cases, the blue curves are steeper than the red curves, illustrating the oblique effect for both perception and pursuit. The σ values are for the best-fitting cumulative Gaussians using Probit analysis (see Experimental Procedures) and are larger for open-loop pursuit because of the shorter integration time. (C and D) Perceptual (C) and open-loop pursuit (D) thresholds for oblique motion plotted against those for cardinal motion. All the data points are above the line of slope 1 and intercept 0, indicating that all observers exhibit an oblique effect for perception and pursuit. Error bars represent the 95% confidence intervals. Although it is tempting to expect a strong correlation between the magnitudes of the two oblique effects across observers, this is not generally the case. Even if perception and pursuit share the same anisotropic direction signal, they are also affected by unshared noise sources that can result in different overall thresholds (for a detailed discussion, see Stone and Krauzlis, 2003). The fact that the within-observer confidence intervals are similar in magnitude to the intersubject variability acts to further obscure any correlation.

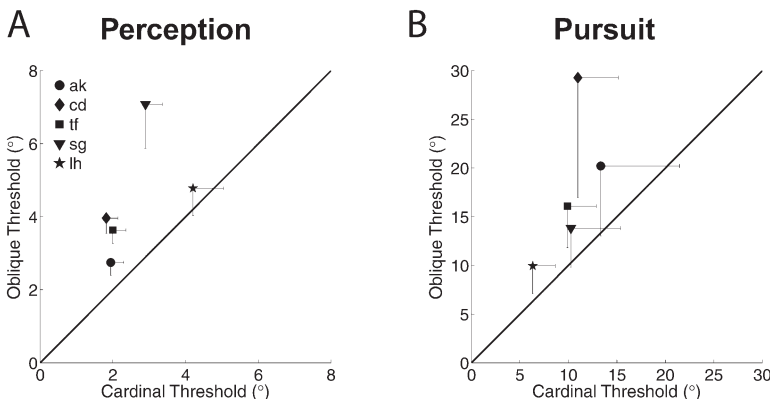


Figure 4. Perceptual and Pursuit Thresholds from Experiment 2

(A) Perceptual thresholds for oblique motion plotted against those for cardinal motion. (B) Pursuit thresholds for oblique motion plotted against those for cardinal motion. In both cases, all the data points are above the line of slope 1 and intercept 0, indicating an oblique effect for both perception and pursuit. Error bars represent the 95% confidence intervals.

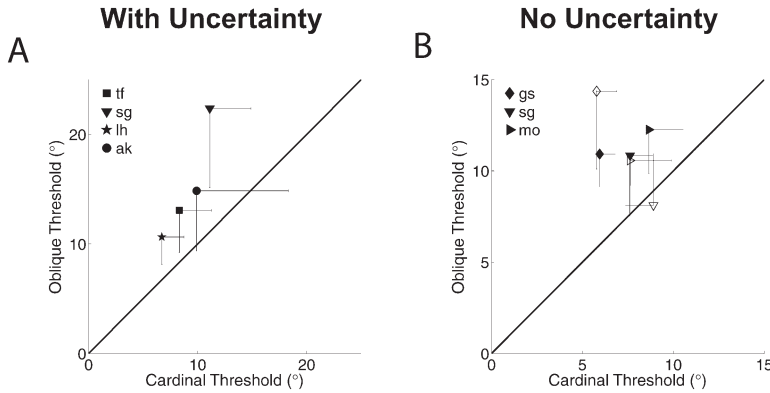


Figure 5. Pursuit Thresholds for Experiments with No Perceptual Task

(A) Pursuit thresholds for oblique motion plotted against those for cardinal motion for experiment 3, in which there was significant directional uncertainty. All the data points are above the line of slope 1 and intercept 0, indicating an oblique effect. (B) Pursuit thresholds for oblique motion versus those for cardinal motion for experiment 4, in which there was no directional uncertainty. Closed symbols represent thresholds from an analysis of the entire experiment, which included all eight canonical directions, and the open symbols indicate a restricted analysis of the three directions (leftward or 180°; downward or 270°; and leftward and downward, or 225°)

used in Churchland et al. (2003). All the closed symbols lie above the line of slope 1 and intercept 0, indicating an oblique effect. For the open symbols, one subject crossed the line, and the statistical significance of the oblique effect across observers was lost. Throughout, thresholds and 95% confidence intervals are the median values across 20 Monte Carlo simulations of different possible 2-IFC runs (see Experimental Procedures).

locked to the cardinal directions due to the strong peaks at the four cardinal directions. The mean amplitude (\pm SD across observers) of the fourth harmonic (normalized by the dc component) was $40\% \pm 10\%$ and the phase was $-1.9^\circ \pm 2.5^\circ$. Thus, across observers, the alignment of the peak direction gain was statistically indistinguishable from the ideal cardinal directions [$t(3) = 0.679$, $p > 0.546$; two-tailed].

The middle column of Figure 7 shows the direction noise as a function of target direction. There is little systematic variation across directions (except for ob-

server sg, who shows a clear horizontal-vertical anisotropy). This finding indicates that the observed overall oblique effect is primarily due to the observed gain effect in the direction coding and not to an anisotropy in the neural noise itself.

The right column of Figure 7 shows the resultant overall oculometric thresholds. The obvious 4-fold symmetry closely matches that of direction gain, except that the troughs of low threshold (or best discriminability) are well aligned with the cardinal directions, and the peaks are well aligned with the primary obliques. The mean phase (\pm SD across observers) of the fourth harmonic component of the threshold was $43.0^\circ \pm 1.6^\circ$ and was statistically indistinguishable from that of the primary oblique directions, for which the mean phase would be 45° [$t(3) = -1.136$, $p > 0.339$; two-tailed]. The modulation of the oculometric threshold was somewhat smaller than the modulation of the direction gain; the mean amplitude of the fourth harmonic (normalized by the dc component) was $31\% \pm 10\%$. This suggests that the noise slightly dampens the modulation of the direction gain and that direction gain might therefore be a clearer measure of the magnitude of the oblique effect than might direction threshold.

The results shown in Figure 7 clearly identify an anisotropy in direction gain as the primary mechanism and a robust measure of the pursuit oblique effect. Indeed, we can use direction gain to examine the effect of task and uncertainty on the magnitude of the oblique effect. Experiments 2 and 3 were identical, except for the presence or absence of a perceptual direction judgment. The mean ratios (\pm SD across observers) of the cardinal to oblique direction gains are shown in Figure 8A. Across the four observers who ran both experiments, there is no difference between these ratios [$t(3) = 0.071$, $p > 0.948$; paired, two-tailed]. On the other hand, experiments 4, 3, and 5 were run with low (or no), medium, and high values of directional uncertainty, respectively. The mean gain ratios (\pm SD across observers) for these three levels of uncertainty are shown in Figure 8B. Due to both a monotonic increase in gain in cardinal directions and a monotonic decrease in oblique direction gains, the mean ratio shows a borderline significant

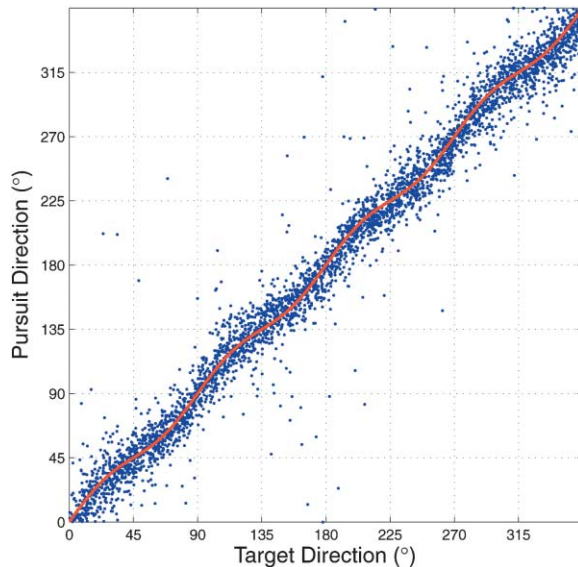


Figure 6. Pursuit Direction versus Target Direction for Naive Observer lh from Experiment 5

The data form a thick wiggly line of average slope ~ 1 . The thickness is a measure of internal direction noise. The slope is a measure of internal direction gain. Note the clear modulation in the slope as a function of direction, while the thickness appears uniform. The solid red trace represents the best-fitting curve with perfect sinusoidal modulation of the unity slope, i.e., Pursuit Direction = Target Direction + $\alpha/4 \times \sin(4 \times \text{Target Direction})$, with the single parameter $\alpha = 0.38$ (the amplitude of the slope modulation) for this observer.

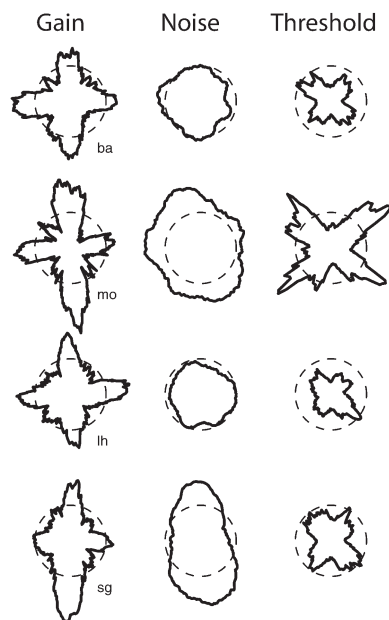


Figure 7. Signal and Noise Underlying the Oblique Effect

Polar plots of direction gain (left column), direction noise (middle column), and pursuit threshold (right column) for experiment 5. Note that all four observers show cloverleaf patterns of threshold, with the peak threshold aligned with the primary oblique directions, while all four observers show a cloverleaf pattern of direction gain, with the peak gain aligned with the cardinal directions. Three of the four observers show little or no variation of direction noise with absolute direction, while the fourth (sg) shows a strong vertical-horizontal asymmetry (that cannot account for the 4-fold symmetry of his pursuit thresholds). Dashed lines represent a gain value of 1 (left column), noise level of 7.5° (middle column), and a direction threshold of 30° (right column).

monotonic increase with increasing uncertainty [one-way ANOVA, $F(2,8) = 3.811$, $p = 0.069$; unfortunately, because different observers ran these three experiments, we could not use a more powerful paired test]. The trend in Figure 8 strongly suggests that the warping of direction space is somewhat dependent on observers' a priori knowledge of what directions might appear in a particular experimental protocol.

Discussion

When perceptual and oculometric direction discrimination thresholds were measured simultaneously, we found an oblique effect in both the perceptual and associated pursuit responses for all 12 observers tested. The pursuit oblique effect remains robust under a wide range of experimental conditions. Furthermore, we found that the degree of anisotropy for pursuit is similar to that for perception. These findings provide strong evidence that perceptual and oculomotor performance is limited by a shared anisotropic visual cortical motion signal that is directionally biased to emphasize the cardinal directions. Furthermore, although our data in experiment 4 clearly demonstrate the existence of an oblique effect even without a perceptual task and without directional uncertainty, we have shown that the magnitude of the oblique effect appears smaller when directional uncer-

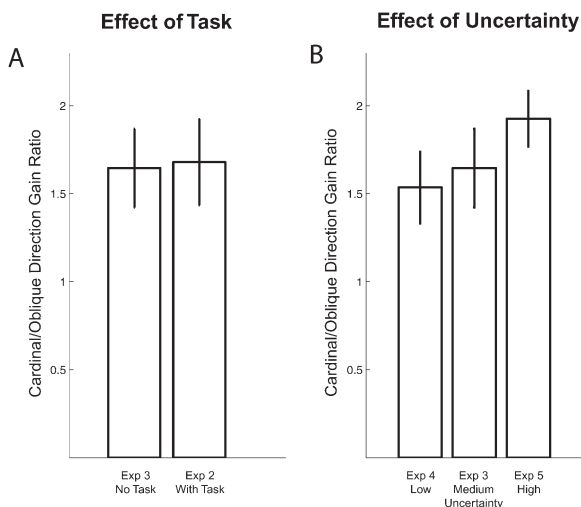


Figure 8. The Effect of Task and Uncertainty on Direction Gain

(A) Mean (\pm SD across observers) ratio of the direction gains for cardinal and oblique directions for experiments with a direction discrimination task (experiment 2) and with no task (experiment 3), both with similar amounts of direction uncertainty. Note that there is little or no effect of task. (B) Mean (\pm SD across observers) ratio for experiments with no directional uncertainty (experiment 4), medium amounts of directional uncertainty (experiment 3), and high amounts of directional uncertainty (experiment 5). Note that the mean gain ratio increases monotonically with increasing uncertainty.

tainty is low, but is unchanged by the presence or absence of a perceptual task.

A recent study of the directional tuning of pursuit onset (Churchland et al., 2003) failed to find an oblique effect for pursuit, although it did document a perceptual oblique effect in the same observers. The discrepancy between their findings and ours is likely due to a number of factors. Estimates of pursuit threshold in the open loop period are noisier than those of perceptual threshold (compare error bars in Figure 3C versus Figure 3D and in Figure 4A versus Figure 4B) even when the latter are made using brief presentations (Krukowski et al., 2003), so that greater statistical power is needed to detect an open-loop pursuit oblique effect. Churchland et al. (2003) used a paradigm with little or no stimulus uncertainty, making the oblique effect smaller and harder to detect. Furthermore, they only examined three arbitrary reference directions, rather than the full set of cardinal directions and principal obliques. These (and other) methodological choices served to reduce the statistical power of their data and to make their analysis more vulnerable to idiosyncratic directional variations in pursuit performance that can be superimposed on a systematic oblique effect, as in the case of observer sg (see Figure 7). Indeed, when we limit our analysis in experiment 4 to the same three directions used by Churchland and colleagues, observer sg's pursuit oblique effect becomes hidden, and the pursuit oblique effect across observers fails to reach significance (Figure 5B, open symbols).

A number of studies have demonstrated that higher-order perceptual and cognitive factors play a central role in the pursuit response and that retinal motion alone cannot account for the response (e.g., Steinbach, 1976;

Kowler, 1989; Dobkins et al., 1998; Beutter and Stone, 1998, 2000; Watamaniuk and Heinen, 1999; Stone et al., 2000; Krauzlis and Adler, 2001; Barnes et al., 2002; Stone et al., 2003; Madelain and Krauzlis, 2003; Stone and Krauzlis, 2003; for a review see, Krauzlis and Stone, 1999). In particular, it has been well established that expectation and prediction (e.g., Kowler, 1989; Barnes et al., 2002) play a strong role in shaping smooth eye movement responses. Our data suggest a mechanism by which the amount of a priori knowledge of stimulus direction can directly affect the direction of smooth pursuit. The fact that, on average, the magnitude of the modulation of direction gain was monotonically related to the degree of stimulus uncertainty present in the task suggests that the warping of direction space is shaped by higher-order signals.

Given that the perceptual and pursuit oblique effects are also present during steady-state pursuit (see also Krukowski et al., 2003), the oblique effect is not linked to motion direction on the retina, but rather to target direction in head-centered (or world-centered) coordinates. MST is the earliest cortical area that has been shown to combine retinal slip and pursuit signals (Newsome et al., 1988), presumably to reconstruct a signal related to target motion in head-centered (or world-centered) coordinates (Stone et al., 2000; Ilg et al., 2004). Thus, it seems highly likely that the neural locus that limits both perceptual and pursuit performance (and is responsible for the oblique effect) is in or downstream from MST. This view is consistent with findings that the preceding cortical area MT appears to have receptive fields exclusively in retinal coordinates (Newsome et al., 1988) and does not appear to show any signs of an oblique effect (Churchland et al., 2003) and that MST is clearly involved in both perception and pursuit (Dursteler and Wurtz, 1988; Komatsu and Wurtz, 1988, 1989; Pasternak and Merigan, 1994; Celebrini and Newsome, 1995; Rudolph and Pasternak, 1999; Ilg and Theier, 2003). Our data, in conjunction with these previous findings, restrict the neural locus of the oblique effect for motion direction so that it must be at or after the point where retinal and extraretinal signals are combined, but before the divergence of perceptual and oculomotor pathways. Our data, together with the recent finding of trial-by-trial correlation between perceptual and pursuit responses (Stone and Krauzlis, 2003), therefore provide strong evidence that direction estimation for both perception and pursuit is limited by a shared neural motion direction signal generated in area MST or later in the visual cortical pathway and that this signal encodes motion direction with an expansion of direction space around the cardinal directions.

Experimental Procedures

Visual Stimuli

The stimulus was a single bright spot presented by back-projection of a red laser light source onto a 30×40 inch tangent, translucent screen. The position of the spot was controlled using a pair of orthogonal mirror galvanometers driven on a millisecond timescale with ~ 0.001 deg spatial resolution by a pair of PCs running Tempo data acquisition and control software. Observers viewed the stimuli at a distance of 73 cm in a dark room with a white background (13 cd/m^2) on the backlit tangent screen. Head movements were minimized by use of a bite bar.

Eye Movement Recording

The position of the observer's left eye was monitored using an infrared, video-based tracker (ISCAN, model RK-726PCI) sampling at 240 Hz. To calibrate the tracker, prior to each run observers fixated a 3×3 grid of points, -10 deg to 10 deg in azimuth and elevation. (For clarity, we use "deg" to denote degrees of visual angle and $^\circ$ to denote degrees of angular direction.) Eye position in tracker coordinates was then converted to eye position on the screen by the best-fitting bilinear function (see Beutter and Stone, 1998). The spatial precision of the tracker was estimated by measuring the standard deviation of eye position fixations during calibration, typically yielding values <0.1 deg.

Saccades were automatically detected by thresholding the correlation between the eye velocity trace and a saccade template. The threshold value was chosen to ensure detection and removal of saccades of ~ 0.3 deg or larger and to ensure that for smaller saccades, which were difficult to distinguish from noise, the saccade detector erred on the side of finding false positives rather than missing true saccades. Eye velocity traces were generated by low-pass digital differentiation of the desaccaded eye position traces (-3 dB at 32 Hz). For experiments 2 through 5, we only considered the presaccadic pursuit responses for analysis. (For experiment 1, this was not possible, because there was always a large early saccade, due to the fact that target motion was tangential to the fixation point.) For three of the observers in experiment 2, we performed a separate subjective analysis with saccades detected and removed by visual inspection of all trials. The results were qualitatively the same.

Experimental Design

Experiment 1

The stimulus moved at 10 deg/s for $800 \pm 50 \text{ ms}$ along a straight path tangential to an invisible ~ 5 deg radius circle (Figure 1A). Observers were presented with two sequential intervals of stimulus motion: a standard at one of eight canonical directions (four cardinals: 0° , 90° , 180° , and 270° ; and four primary obliques: 45° , 135° , 225° , and 315°) jittered by $\pm 3^\circ$ and a test differing from the standard by $\pm 2^\circ$, $\pm 4^\circ$, $\pm 6^\circ$, or $\pm 8^\circ$. On each trial, the duration and direction were randomly chosen, as was the presentation order of the test and standard intervals.

A number of steps were taken to eliminate extraneous cues that could influence performance. The midpoint of each trajectory, for each interval independently, was randomized by ± 2 deg in eccentricity and by $\pm 7^\circ$ in radial position about the ideal tangent point on a 5 deg radius invisible circle. (This corresponds to an initial step size ranging from 4.8 deg to 8.2 deg.) Furthermore, the directional jitter described above minimized the usefulness of the absolute direction of any single interval, which might otherwise have been compared to an internal standard or some peripherally visible feature on the screen or in the room.

Eight observers (five naive) were asked to follow the motion of the dot with their eyes and to report, using a button press, the interval that contained the more clockwise direction of motion (e.g., the blue arrows in Figure 1A). A fixation point appeared before the beginning of each interval, but was extinguished simultaneously with the appearance (and motion) of the target. When the fixation point reappeared between the two intervals of a trial, observers were required to return to within 0.75 deg of this point before the second interval would begin.

For this experiment, because of the slower target speed of 10 deg/s , we ensured that our analysis was restricted to the $\sim 95\%$ of trials with robust pursuit by excluding trials when observers failed to reach an average eye velocity of 2.5 deg/s early in the trial (250 – 400 ms after the onset of target motion). However, our results were qualitatively unchanged if all trials were included in the analysis. For some observers, the steady-state pursuit response gain (eye speed/target speed) varied with direction. However, after the above trial-selection process, averaged across observers, the standard deviation of response gains across directions was only $\sim 8\%$. More importantly, we found no systematic oblique versus cardinal pursuit response gain asymmetry. The average pursuit response gains for the cardinal and oblique directions differed by $<4\%$ for all observers.

Experiment 2

Unless otherwise stated, stimulus conditions were the same as for experiment 1. Observers were presented with two sequential inter-

vals of stimulus motion, although the speed (25 deg/s), duration (450 ± 50 ms), initial step size (3 deg), and trajectory toward the vicinity of the center of the screen were matched to those in Churchland and colleagues (2003) (Figure 1B). All eight canonical directions (0° , 90° , 180° , 270° , 45° , 135° , 225° , 315°) were randomly interleaved, and the choice of test and standard directions relative to these canonical directions was performed as in experiment 1, except that there was no positional jitter, to minimize the occurrence of early saccades. Five observers (four naive) were asked to follow the moving dot with their eyes, and to report, using a button press, the interval that contained the more clockwise direction of motion (e.g., the blue arrows in Figure 1B).

Experiment 3

The stimulus conditions were identical to those of experiment 2 (Figure 1B). Only the first interval of each trial was presented. Four observers (three naive) were asked to track the moving spot, but no psychophysical task was performed. Two of the observers who had previously run experiments 1 and 2 participated, and two new naive observers were included who had no knowledge of the versions of the experiment that included a perceptual task (they ran experiment 2 after running experiment 3).

Experiment 4

Stimulus conditions were identical to those of experiment 3, except that stimulus direction was blocked such that each direction was presented 60 times in a row (Figure 1C). Each of the eight canonical directions and directions $\pm 5^\circ$ off of canonical were presented in separated blocks (for a total of 24 directions tested). Three naive observers were asked to track the moving spot, but no psychophysical task was performed.

Experiment 5

Stimulus conditions were identical to those of experiment 2, except that the standard directions were uniformly distributed around the full circle (Figure 1D). Four naive observers were asked to track the moving spot and to report in which interval the spot moved more clockwise. We observed horizontal-vertical asymmetries in the open-loop pursuit response gains. However, we found no systematic oblique versus cardinal asymmetry. The average pursuit response gains for the cardinal and oblique directions differed by $<6\%$ for all observers.

Psychophysical Data Analysis

Psychometric curves were generated from the percentage of trials for which the test was judged to be more clockwise for each condition (Figure 3A). To increase statistical power and to average out any small idiosyncratic directional effects, psychophysical decisions were combined across all four cardinal directions, across all four oblique directions, and across runs. The resulting psychometric curves were then fit with a cumulative Gaussian function using Probit analysis (Finney, 1971). The direction-discrimination threshold was computed by dividing the best-fitting standard deviation by $\sqrt{2}$ to compensate for the fact that there were two stimulus intervals. The 95% confidence interval for each estimate of threshold was calculated, using χ^2 statistics (Press et al., 1992).

Oculomotor Data Analysis

Pursuit data collected during each 2-IFC trial were converted into a binary "oculometric" decision (see Beutter and Stone, 1998; Stone and Krauzlis, 2003). For each trial, if the pursuit direction in the analysis interval of the test presentation was in a more clockwise direction than that of the standard presentation, the oculometric decision was considered "clockwise." Conversely, if the opposite was true, then the oculometric decision was deemed "counterclockwise." Example pursuit traces and oculometric decisions are shown in Figure 2. Once these decisions were determined for all trials, an "oculometric" curve could then be derived (Kowler and McKee, 1987), completely analogous to the psychometric curves, in which the percentage of clockwise decisions is plotted against the difference between test and standard stimulus directions (signal strength) as seen in Figure 3B. The oculometric decisions were combined across runs and across cardinal (or oblique) directions, and the resulting oculometric curves were fit using Probit analysis, just as for the psychometric curves.

The oculometric curves were generated in a slightly different fash-

ion for experiments 3 and 4, because only single intervals of stimulus motion were presented for each trial. Rather than determining the oculometric decisions based on comparison of actual test and standard stimulus pairs, oculometric decisions were based on a Monte Carlo simulation of a 2-IFC, using randomly selected pairs of trials. Pairing was done exclusively within runs to avoid any artifacts caused by small differences in calibration across runs, but the resulting oculometric decisions were then pooled across runs and fit using Probit analysis, just as with the true 2-IFC data. The reported oculometric thresholds and confidence intervals were the median values across 20 iterations. For the oculometric thresholds in experiment 5, a similar process, adapted to handle the continuum of possible reference directions, was used. To be comparable with the single-interval experiments 3 and 4, pursuit threshold for a particular direction was calculated by generating an oculometric curve, using all combinations of first interval directions within a moving 30° window. The window was moved in 1° steps around the full 360° circle to generate the polar plots in Figure 7.

The temporal interval used for our open-loop oculometric analysis was based on estimates of pursuit latency for each observer. Latencies were estimated by fitting an elbow function to polar speed traces averaged across the responses to the first intervals of all trials. For experiment 1, the mean latency (\pm SD across observers) was 184 ± 16 ms, as expected for stimuli with high spatial and directional uncertainty (Stone and Krauzlis, 2003). For experiments 2, 3, and 5, the mean latencies were 144 ± 8 ms, 143 ± 11 ms, and 143 ± 3 ms, respectively, as expected for the faster target speed. For experiment 4, the mean latency was lower still: 110 ± 10 ms, given the lack of directional uncertainty. For experiment 1, the open-loop analysis interval was therefore set to be the first 150 ms of pursuit. For experiments 2–5, we used the first 90 ms of presaccadic pursuit to match the open-loop analysis interval of Churchland et al. (2003).

Direction Gain and Noise Calculations

For Experiments 3 through 5, direction gain was calculated as the local slope of plots of pursuit direction versus target direction. The gain at a particular target direction was calculated as the slope of the best-fitting line to the data for target directions within a 30° window of the particular noise direction. Direction noise was calculated as half the difference between the 25th and 75th quartiles (JND) within a much smaller direction window (3°) in order to avoid effects of direction gain bleeding into the noise calculations. The noise data were then boxcar filtered with a 30° window to provide comparable smoothing to the gain data.

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